

CONSPECIFIC INTERACTIONS IN THE LYCOSID SPIDER *RABIDOSA RABIDA*: THE ROLES OF DIFFERENT SENSES

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ABSTRACT. The behavior of sighted and of blind male and female *Rabidosa rabida* paired in various combinations was videotaped and analyzed. When walking, neither sighted nor blind spiders could detect motionless conspecifics prior to contact. When motionless, blind males detected moving females at greater distances than they detected moving males. However, neither sighted nor blind motionless males detected very slowly moving females at any distance. These data suggested for *R. rabida*: (1) the effectiveness of visually and vibrationally cryptic locomotion, (2) a lack of form vision, and (3) absence of a close-range, air-borne pheromone. In both sexes, visual detection of moving conspecifics by motionless spiders provided for accurate orientation responses at greater distances than did mechanoreception. Nonetheless, blind females could orient accurately toward courting males at close range based on vibrations. Blind males showed courtship display when briefly contacted by another male, suggesting an inadequate chemically based sex-recognition mechanism. Sighted males showed courtship display after visually detecting a walking male, but did not do so in response to a courting male, i.e., mutual courtship did not occur. Blind males sometimes did perform mutual courtship, suggesting an inadequate vibratory recognition mechanism. Unlike salticids, these lycosids did not require vision to initiate either agonistic display or ritualized fighting.

To the human observer, wolf spiders usually appear to be responding to one another on the basis of visual information. Indeed, the use of video image presentation in studies of certain species of *Schizocosa* Chamberlin 1904 by McClintock & Uetz (in press) and E. Hebets & G. Uetz (unpubl.) have demonstrated that some lycosid spiders can rely primarily on visual cues to mediate intraspecific interactions. The roles of different pairs of eyes in such responsiveness by the lycosid spider *Rabidosa rabida* (Walckenaer 1837) also have been elucidated by video playback (Rovner 1993).

Nonetheless, under natural conditions, when two spiders located close to each other share the same substratum, the possibility that mechanoreception plays the predominant role must be kept in mind. In related work, the latter was shown to be the case for interspecific interactions involving wolf spiders (*Rabidosa rabida*) that prey on fireflies (*Photuris* spp.) (Lizotte & Rovner 1988), for which it had previously been assumed that such predation was primarily visually based. The extreme sensitivity of the spider's metatarsal lyriform organs (slit sensillae) and trichobothria, both of which detect vibrations, has been well

documented (Barth 1985; Reissland & Görner 1985).

In the present study I sought to determine the relative importances of vision, mechanoreception, and chemoreception for mediating conspecific interactions in the lycosid spider *Rabidosa rabida*. To do this, I compared the behavior of sighted spiders to the behavior of blind ones. Both male-female and male-male encounters were included in this investigation.

I chose *R. rabida* for the present study because all three channels of communication have been demonstrated to be used by this species. The adult males (unlike immature males and females of all instars) possess black legs I and silvery-white palpal tarsi, both of which are waved in stereotyped patterns during courtship display (Kaston 1936; Rovner 1968). Video playback of this behavior revealed that the leg I extension component triggers each bout of the female's receptive display (Rovner 1993). On the other hand, in the male's courtship display, the inclusion of an acoustic signal, which by itself can trigger each bout of receptive display in females (Rovner 1967), plus the occurrence of mating and other behaviors during nighttime as well

as daytime (*ibid.*) indicate that vision should not be assumed to be the most important sense used by this species. In addition, one must consider the possible roles of chemical signals, since a contact sex pheromone present on the female's dragline is known to play an important role in the male's search for the female (Tietjen 1977).

METHODS

The species used in this study was the subject of numerous papers during the previous three decades that examined various aspects of communication, reproduction, and prey capture. In those papers the species name was given as *Lycosa rabida* Walckenaer. In the present study the name *Rabidosa rabida* (Walckenaer) is used, in light of the recent revision by Brady & McKinley (1994).

Penultimate *R. rabida* were collected in late June 1991, 1992, and 1993 in Athens County, Ohio, USA. Voucher specimens of the resulting adults have been deposited in The Field Museum, Chicago.

The methods of maintenance and the laboratory conditions during data collection have been described previously (Rovner 1989). Spiders were not paired for observation until one week after their final molt. Each individual was used once, so that none would be affected by the experience of a prior encounter with a conspecific. Observations were made at various times of the day between 1000 h and 2200 h.

To cover the eyes of spiders, I painted them with two coats of dark-colored, water-based enamel (Top Color Hobbylack, Pelikan AG). That this ensured complete occlusion had been established previously (*ibid.*). Spiders that had been blinded were used in data collection one or more days after undergoing the occlusion procedure.

For data collection, each pair of spiders was introduced into a glass-topped wooden cage (125 mm × 100 mm × 35 mm high; a fresh piece of paper substratum was placed on the floor of the arena for each trial). Several minutes elapsed between the introduction of the first and second spiders. Behavior was recorded on videotape (Sony SL-HFR70 videocassette recorder). The camera (JVC GX-8NU) was aimed at a front-silvered mirror that was located 0.5 m above the arena floor and which had been fixed at a 45° angle to the arena floor.

This yielded a dorsal view of the spider, which facilitated the later measurements of distances between spiders and of turning angles (accurate to the nearest 5°). Substratum vibrations were recorded on the audio track by use of a vibration pickup system (General Radio 1560-P14) connected to a sound-level meter (General Radio 1551-C), whose output was fed into the video camera.

For male-female interactions, 10 males and 10 females were used in 10 trials for each of four types of pairings: sighted male-sighted female; blind male-sighted female; sighted male-blind female; and blind male-blind female. Thus, the behavior of 40 males and 40 females heterosexually paired was recorded and analyzed.

For male-male interactions, 20 males were used in 10 trials for each of three types of pairings: sighted male-sighted male; blind male-sighted male; and blind male-blind male. Thus, the behavior of 60 males encountering other males was recorded and analyzed.

I arbitrarily used the distance between the faces of the two spiders as the basis for measuring the distance between individuals. To help the reader visualize the distances, they are first roughly given as approximate body lengths, rounded to the nearest 0.5 body length (MBL = male body lengths; FBL = female body lengths) and then, more precisely, in mm. Males averaged 12 mm in length; females, 18 mm. (Because of the limited size of the arena, a size chosen to provide sufficiently detailed images of the spiders via the fixed video camera, the maximum possible distances over which some visual responses could be elicited were not determined. The reader will be reminded of this by my use of the phrase "at distances of up to at least. . .").

Because only the largest distances and turning angles observed were the data of interest with regard to assessing the relative effectiveness of the various signals and receptors involved in the spiders' interactions, only the maximum values are given in this paper for the various data sets. Another reason for not using mean values was that the distances and turning angles associated with interacting spiders were highly variable (non-normally distributed). This was because, unlike an experiment in which investigator-controlled stimuli are presented to a single test spider from one or two predetermined directions, the locations

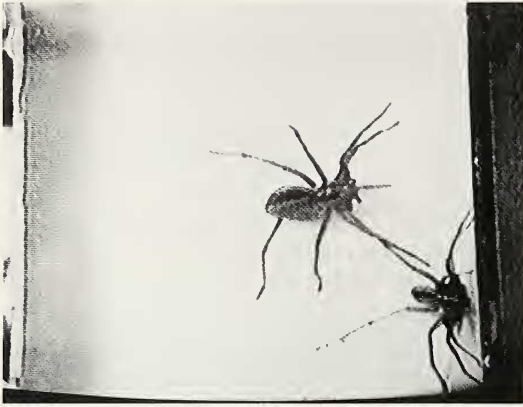


Figure 1.—The stationary, sighted male *Rabidosia rabida* (at right) did not respond to the slowly wandering female as she approached, resulting in the overlap (but not contact) of the female's right leg II and the male's left leg IV. (In this and all other figures, the spiders are on the horizontal arena floor being viewed from above.)

and orientations of freely roaming spiders at the onset of a response by either of the spiders were unpredictable, as were the amplitudes of stimulating vibrations or movements produced by each member of the pair at any one moment.

One other category of data will be provided in this paper. For male-male interactions, the proportion of spiders (within each group of pairings) that showed a particular behavior is given parenthetically as a percentage (e.g., 13 of 20 males = 65%).

MALE-FEMALE INTERACTIONS

Stationary male approached by a female.—Both sighted and blind motionless males occasionally failed to respond to females that wandered very slowly toward them and got so close (2 MBL (26 mm) or nearer) as to have overlapping legs (Fig. 1). Usually, however, blind males turned toward a female approaching from any direction at a distance of up to 4 MBL (46 mm), as did sighted males at even greater distances.

Motionless males sometimes responded to an approaching female by a withdrawal response, either backing up a short distance or running away rapidly. These responses were triggered at distances of up to about 4.5 MBL (52 mm) in sighted males. If the male was courting, his typical response to a female that approached to within 3 MBL (37 mm), es-

pecially to a female performing a receptive display (Rovner 1967), was to suddenly "lean back" and to increase the flexure of legs I, thereby pulling himself into a "tightened" courtship posture. He subsequently also shortened the distance covered by his leg I during the leg extension component of courtship, resulting in an "abbreviated leg extension." The effect of both changes was to reduce the possibility of contacting the female during courtship. In this species, contact resulting from courtship is initiated by the female, never the male (Rovner 1968). It is of interest that, at a closer approach distance (2 MBL, 22 mm), blind courting males also switched to a tightened courtship posture and abbreviated leg extensions.

Stationary male detecting a non-approaching female.—If the female performed a turn or walked at a perpendicular or oblique angle to the motionless male's body axis (at a faster than cryptic speed), the male usually responded by a full turn to face directly toward her. This occurred in sighted males at up to at least about 5 MBL (61 mm), but in blind males at only up to about 2 MBL (22 mm). Blind males could respond at greater distances of up to about 4 MBL (46 mm), but only with partial turns, i.e., they were not yet facing the female at the completion of the turn. Thus, vision provided for a more accurate orientation response at a greater distance than did mechanoreception.

Moving male encountering a cryptically moving or motionless female.—When wandering, neither sighted males nor blind males could detect very slowly moving or motionless females. Males often approached such females to near or actual contact, even if the female adopted a vertical extend agonistic posture (Nossek & Rovner 1984) during the male's approach (Fig. 2). Such data suggested that moving males could not readily detect stationary females performing postural and/or appendage position changes and that they lacked form vision. Also, there apparently was no close-range, airborne pheromone produced by the female. On the other hand, if the wandering male *R. rabida* finally contacted the female, he began courtship display within 0.3 sec. (Since males did the same after contacting other males, as described below, it was not certain that courtship onset following hetero-



Figure 2.—The wandering, sighted male *Rabidosia rabida* (at right) continued to approach the female, even though she performed the behavior of adopting a "vertical extend" posture while both spiders were nearly face to face during his approach.

sexual contact was dependent on a sex pheromone.)

Sighted stationary female responding to a moving male.—Sighted females performed full turns of up to 155° in response to the stimulus of a male walking across their field of view at distances of up to at least about 4 FBL (68 mm). They also performed such turns in response to the first leg I extension movement shown by a male that had just begun courting at up to at least about 3 FBL (55 mm) distance.

However, sighted females sometimes showed no response to the approach of a wandering male at what seemed to be greater than cryptic speed coming from any of various directions. This resulted in the male almost contacting her nearest leg before she performed a flexion of that leg or some stronger response. In such cases, the female's response was triggered when the male's leg I swept past her leg at 2–3 mm distance between surfaces. (Trichobothria probably were the receptors that detected the stimulus.) Occasionally, actual contact between the male and female legs occurred before the female responded.

Such near or actual contact between the spiders was least likely to occur when a wandering male waving his legs I happened to approach directly toward the female's face. When a leg I-waving male made such an approach toward the female and was about 1–2

FBL (21–32 mm) away from her, the female typically drew back into a horizontal flex posture (Nossek & Rovner 1984). If the male got closer (i.e., less than 1 FBL away) without initiating courtship, the female usually ran rapidly forward in an apparent attempt to capture him.

Such high-speed approaches by the female elicited a rapid running away by the male. Advancing females usually did not respond by turning in the direction of the departing male, but instead remained oriented toward the male's original location, toward which she had been running. In other words, the female failed to perform re-orientation responses that would have tracked the escaping male's rapidly changing location as he dashed to a new site in the arena. It is probable that, because of the female's own movements, her visual system could not perceive the rapid re-location of the fleeing male. Nonetheless, a few of the sighted females were able to pursue an escaping male.

Blind stationary female responding to a moving male.—Blind motionless females could detect walking males at up to only about 2 FBL (33 mm) distance. They also were more likely than sighted females to be involved in near or actual contacts by such males, since these females often did not respond to an approaching male unless directly contacted or unless his waving leg I swept to within 2–3 mm of one of their legs. Consequently, blind females sometimes were unresponsive to extremely close approaches by slowly wandering males (Fig. 3). On the other hand, a courting male was detected by blind females at up to at least about 3 FBL (58 mm). The females' response to such vibratory input was usually a partial turn, but sometimes they performed a full turn of up to 140° that resulted in their directly facing the male. This ability to use mechanoreceptive information for accurate orientation toward a stimulus located at a distance comparable to that for visually based orientation is dependent on the nature of the source, a courting male, whose acoustic signal exceeds the vibration amplitudes generated by a walking male.

In this study, blind females solicited and accepted copulation more readily than did sighted females: 90% (18/20) of the blind females copulated; 60% (12/20) of the sighted females copulated. A *t*-test of the arcsine-transformed



Figure 3.—The blind female *Rabidosa rabida* (facing right) remained motionless in a rest posture as the slowly wandering sighted male approached so closely that his legs I and II overlapped (but did not contact) her left legs and body.



Figure 4.—Blind male *Rabidosa rabida* displaying courtship toward one another following a brief contact.

percentages was significant at $P < 0.05$ ($t = 2.30$). Also, three of the sighted females cannibalized the male rather than permit copulation, while none of the blind females preyed on the male. Does the availability of the visual channel in the female increase the likelihood that she will respond to a non-courting male by an act of attempted predation? Or perhaps is the female being more selective ("chooser") in response to some type of visual information than she would be if her response were based purely on vibratory information?

MALE-MALE INTERACTIONS

Inability to detect cryptically moving or motionless individuals.—As noted above for male-female interactions, contact typically resulted from the inability of either blind or sighted spiders when wandering to detect a motionless spider at any distance, even one that adopted a horizontal flex posture when it was approached closely. Furthermore, when motionless, most of the blind spiders (65%), and even some of the sighted ones (35%), did not respond to a wandering spider that approached very slowly. Thus, accidental encounters were frequent, as were cases in which both spiders ended up in resting positions with overlapping but non-contacting legs. The latter occurred more commonly in pairings in which both spiders were blind than in pairings of sighted spiders, although the amount of resultant leg overlap was no dif-

ferent (sighted: 7.4 ± 0.92 mm ($n = 12$); blind: 8.4 ± 0.89 mm ($n = 17$), Mann-Whitney $U = 86$, $P > 0.05$). Thus, if the conspecific was motionless or moving very slowly, the onset of courtship or agonistic display required contact or near contact, even for some sighted spiders.

Accuracy of orientation turns.—If a motionless spider detected a moving conspecific, blind males were less able than sighted males to accurately perform a full turn to face the stimulus. In other words, most of the blind males (70%) performed partial turns. The proportion of orientation turns that reached the target direction was 39% (31/79) in blind males but almost twice that (75% = 38/51) in sighted males (for arcsine-transformed percentages, $t = 4.10$; $P < 0.001$). These data suggested that detection of distant vibrations via the metatarsal lyriform organs did not yield as precise an orientation response in male *R. rabida* as did visual input.

Courtship display as an initial response.—In 70% of the pairings that involved a sighted male, courtship display followed the sighted male's orientation toward the other male. In 50% of the pairings involving blind males, courtship display was the initial response of a blind male to brief contact or near contact (i.e., 2–3 mm between leg surfaces). Mutual courtship display was sometimes the initial interaction when two blind males encountered each other (Fig. 4); however, this did not occur when sighted males were involved, i.e., a sighted male did not court in



Figure 5.—Male *Rabidosa rabida* engaged in grappling, which involves pushing one another while maintaining prolonged contact of their legs I. Although not visible in this video image, the defensive mechanism of leg spine erection occurs in both spiders throughout such contact.

response to a courting male. These data indicated that: (1) As was probably true of females, males lacked a visual recognition mechanism for determining the sex of a conspecific that had not yet begun courtship display. (2) Males lacked a chemical recognition mechanism that sufficed for determining the sex of another male on the basis of a brief contact. (3) Once courtship had begun, the visual system was more effective than the mechanoreceptive system for recognizing that a conspecific was a male, i.e., seeing the leg I extension component of courtship display probably was a more effective source of information than was detection of the concurrent palpal-generated vibrations.

Agonistic display.—When one male did recognize that a nearby conspecific was also a male, the first male initiated agonistic display (Rovner 1968). Such recognition of the sex of the other spider could come from detecting the visual or acoustic components of a courting male's display. However, recognition was especially likely to result from the prolonged period of contact that occurred during "grappling," which was ritualized fighting characterized by mutual pushing while holding each other's legs I (Fig. 5).

The palpal-generated sounds characterizing agonistic display were louder than those produced during courtship display. On the basis of these agonistic display sounds, blind males

could detect other males at a distance of up to at least 4.5 MBL (56 mm). This indicated that when the sighted males had responded to another male's agonistic display, I could not know if the response had been elicited primarily on the basis of vision or mechanoreception.

Lack of importance of vision for dominance.—In the 10 trials involving a sighted male paired with a blind male, the blind male turned out to be dominant in seven of the nine trials in which dominance was clearly established. (In these seven trials, the blind male was the larger individual in two trials, equal in size in four trials, and smaller in one trial.) The onset and nature of grappling behavior was similar in sighted and in blind males, and thus probably was mediated entirely by mechanical information during contact.

DISCUSSION

By experimentally shutting off the visual channel of information gathering, I was able to examine the effectiveness of the mechanoreceptive and chemoreceptive channels for mediating interactions between individuals of *R. rabida*. At distances of up to four male body lengths (46 mm), a blind motionless male could detect the vibrations of and accurately orient toward a female that was walking at a greater than cryptic speed. The detection of the presence of another male, whose lighter mass generated lower amplitude vibrations than did a female, tended to yield less accurate orientation, with partial turns occurring rather than full turns. Nonetheless, the ability of blind males to detect conspecifics at a distance and to perform withdrawal responses when females approached indicates that, whenever anyone is studying the interactions of wandering spiders, the responses of sighted males to conspecifics cannot be assumed to be visual but instead may be based partly or entirely on substratum vibrations. Over many years of observing this species, I had assumed that the tightened courtship posture and abbreviated leg extension were visually based responses. (Of course, at the greater distances at which they were shown by sighted males, they probably are visually based responses.) The point is that no conclusion as to which sense mediates a response can be drawn by simple observation of wolf spiders. An experimental ap-

proach eliminating one or the other sense is required.

The behavior of blind motionless females also was revealing. The distance at which they could detect walking males was less than half the distance achieved by sighted females. However, blind females could detect a courting male at almost twice the distance they could detect a walking male. Assuming that vision is inadequate under dim light (but see below), the relatively high-amplitude, patterned vibrations generated by a courting male would enable him to be identified at night by a female at a greater distance than that at which she could detect a wandering male.

Blind motionless females sometimes did not detect males that approached slowly. However, actual contact usually was avoided, probably because the female's trichobothria were stimulated by the wandering male's leg I waving at a near-field distance of 2–3 mm. This probable role for the trichobothria might have gone unnoticed by investigators working with sighted females, since the female's reaction would have been assumed to be based on visual stimulation.

A lack of form vision in *R. rabida* was suggested by the behavior of motionless sighted males, which "ignored" very slowly moving females. (Of course, the female avoided detection by being both vibrocryptic and visually cryptic.) Also providing evidence for a lack of form vision was the fact that wandering, sighted males approached and contacted stationary females. Males even continued to approach females that adopted a vertical extend posture when the male came within close range. This lack of response to the female's action may be due to the probability that a moving *R. rabida* does not readily detect a moving stimulus, which also was suggested to be the reason for the absence of a mirror-image response in these spiders (Rovner 1989). Such data call into question the widespread assumption that the defensive postures seen in many spiders, such as *R. rabida*'s vertical extend, are displays, i.e., behaviors that evolved partly or wholly for communication. Instead, in some species they may still serve purely to prepare the spider to use its chelicerae and fangs.

An unexpected finding of this study was the ineffectiveness of chemoreception for providing information about the sex of a conspecific.

Unlike the females of various salticid spiders (Crane 1949), female *R. rabida* apparently do not produce an olfactory signal that enables males to detect females at close range (Fig. 3). (Tietjen (1979) had experimentally demonstrated the absence of a long-range olfactory pheromone in this species.) Actual contact was needed for a wandering male to be stimulated to court by a motionless female. Since males also showed courtship after briefly contacting other males, it is possible that *R. rabida* has a species-specific rather than a sex-specific pheromone. Or perhaps if contact is too brief, the opportunity for uptake of a pheromone by chemoreceptors is inadequate to provide for recognition. Then again, it is also possible that mechanoreception by itself can cause courtship onset.

What may be concluded overall about *R. rabida* is that vision (primarily) and mechanoreception (secondarily) play important roles in mediating interactions under daylight conditions, while the chemical sense may not be involved unless there is prolonged contact with a pheromone-bearing surface. The behavioral evidence obtained in the present study supports Land's original (1981) view that lycosids lack form vision. However, Suwa (1984) hypothesized that females of the lycosid species *Pardosa laura* Karsch 1879 use form vision for species discrimination. Of particular significance are recent physiological studies by Land & Barth (1992) and Strausfeld et al. (1993) on the related ctenid spider *Cupiennius salei* (Keyserling 1877), which point to a role for form vision via the principal (antero-median) eyes. Consequently, the possible involvement of form vision in mediating interactions in *R. rabida* and other lycosids must be explored in future behavioral investigations.

Data in the present study indicate that *R. rabida*'s visual system provides for more accurate directional information-gathering at a greater distance than does mechanoreception. Furthermore, the occurrence of mutual courtship in blind males but not in sighted males suggests that vision provides a more effective recognition mechanism than does mechanoreception. Nonetheless, the data obtained in the blind male-sighted male pairings show that mechanoreception alone is sufficient for the establishment and maintenance of dominance in *R. rabida*. Also, one would assume

mechanoreception to be the primary basis for gathering information about conspecifics during interactions at night. However, behavioral research on *R. rabida* is needed to assess the effectiveness of vision during nocturnal encounters. One must consider the possibility that a dark-adapted visual system in such a lycosid spider could be sensitive enough under very dim light conditions to continue to have the dominant role in mediating interactions that it played under daylight conditions in the present study. It is worth noting that visual sensitivity sufficient for functioning under moonlight has been described for the largely nocturnal ctenid *C. salei* (Barth et al. 1993).

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